Impact of Invertebrate Herbivory on Native Aquatic Macrophytes

by Julie G. Nachtrieb, Michael J. Grodowitz, and R. Michael Smart

PURPOSE: This technical note quantifies the impact that invertebrate herbivores have on native aquatic plants by comparing dry biomass of five macrophyte species between two treatments; an insecticide treatment to remove invertebrate herbivores, and a control where the herbivore complex was left to develop naturally.

BACKGROUND: There is little information available that quantifies the impact of invertebrate herbivores on native macrophyte biomass in the United States. Early research indicated that while macrophytes were useful as substrates for invertebrates and epiphytic growth, they provided little if any nutritive value (Shelford 1918). However, additional studies have shown the importance of macrophytes as a nutritive source for invertebrates. Soszka (1975) found that *Potamogeton* species can lose 50 to 90 percent of their leaf area through insect herbivory and non-consumptive destruction mostly from lepidopterans, trichopterans, and dipterans. Sand-Jensen and Madsen (1989) found leaf area damage to be between 2 and 56 percent for *Potamogeton* species, depending on locality. This damage was primarily attributed to trichopterans and dipterans. Lodge (1991) stated that macrophytes are engaged in aquatic food webs, sometimes to the extent that biomass, productivity, and relative species abundance are dramatically changed by grazers. Finally, Cronin et al. (1998) found that freshwater macrophytes exhibited herbivory similar to that reported for terrestrial plants. These findings countered the conventional idea that aquatic plants offered only surface substrates (Shelford 1918). However, due to the paucity of published accounts of invertebrate herbivory, more research is warranted. For example, a comparison of biomass between grazed and ungrazed macrophytes would add valuable information concerning the role invertebrate herbivores have in aquatic plant communities by providing direct information as to the differences in plant quality, biomass, and dispersal when herbivores are active in a system. Previous studies quantified parameters such as percent herbivore damage to macrophytes, but without a comparison to ungrazed plants, the significance of this interaction is unknown.

Native plants are a valuable component of aquatic habitats. They provide important fish and wildlife habitat (Savino and Stein 1982, Heitmeyer and Vohs 1984, Dibble et al. 1996), improve water clarity and quality, and reduce rates of shoreline erosion and sediment resuspension (Smart 1995). This recently recognized importance has prompted their use in an increasing number of aquatic restoration projects across the United States. However, more information is needed on biological factors that impact their establishment and growth. By understanding all environmental factors that challenge establishment of native plants, we can better design the methodologies needed to overcome these limitations in reservoirs, lakes, ponds, etc.

One major challenge encountered when establishing native vegetation is herbivory. Turtles, crayfish, insect larva, muskrats, nutria, and beaver have been shown to pose a threat to the establishment and growth of aquatic plant communities (Lodge 1991, Dick et al. 1995, Doyle and Smart 1995, Doyle

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et al. 1997). During restoration projects, macrophytes are often planted within cages of various designs to reduce herbivory and biotic disturbance (Smart et al. 1998). Cages are constructed of various sizes and materials and are able to protect macrophytes from crayfish as well as larger herbivores. Yet the current cage design does not exclude invertebrate herbivores. Although not believed to be a major factor in plant establishment in most restoration projects, significant damage by invertebrate herbivores has been seen within cages in several efforts in recent years, including Choke Canyon Reservoir in Texas.[1]

Another reason to examine native macrophyte herbivory is that native plants have been shown to compete effectively against many invasive macrophytes, thereby providing an additional technique to employ as part of long-term management strategies. Some native plants commonly used in the southeastern United States for restoration efforts include *Vallisneria americana* Michx., *Potamogeton nodosus* Poiret., *P. illinoensis* Morong., *Heteranthera dubia* (Jacq.) Small, *and Nymphaea odorata* Ait. Native macrophytes such as *V. americana* have been noted as effective competitors with invasive plants under certain conditions (Smart 1994). By establishing a diverse and hence stable community of native species, the recurrence of aquatic plant problems might be slowed or even prevented.

Many normally non-weedy plants can become problematic in the United States under certain conditions and even more importantly can become serious problems in other countries. Although native to North America, several species of *Nuphar*, *Nymphaea*, and *Potamogeton* are regarded as weeds in northern temperate countries and parts of tropical Africa and Asia (Sculthorpe 1967). *Cabomba caroliniana* Gray, another native species, is becoming a problem in Australia.[2] Rivers, canals, ponds, lakes, and ditches in Great Britain are also being threatened by a non-weedy species in the United States, *Hydrocotyle ranunculoides* L. f. (English Nature 1999). *Ludwigia* spp. are also becoming problematic in many areas of the United States as well as France and other European countries (unpublished data). By understanding the impact U.S. herbivores have on these species new biocontrol agents may be developed for use in the United States and also exported to other countries thereby providing long-term control strategies. Classical biocontrol agents are typically identified by surveys of herbivores and pathogens associated with a host plant in its native range (Purcell et al. 2004). To prevent impacts to non-target species, the potential agent's host specificity and the habitat range of the host are studied (Littlefield and Buckingham 2004). Experiments should also be conducted to determine the ability of the potential agent to control its host plant. If a field release is performed, Schooler et al. (2004) list six criteria to evaluate success of the application:

- Establishment.
- Population increase.
- Spread of the agent.
- Damage.
- Response of the host plant.

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[1] Personal communication. 2006. Dr. Gary O. Dick, U.S. Army Engineer Research and Development Center, Lewisville, TX.
[2] Personal communication. 2006. Dr. Mic Julien, CSIRO Entomology, Long Pocket Laboratories, Queensland, Australia.

- Change in the local plant community.

This research investigated interactions of invertebrate herbivores with five species of aquatic plants: *V. americana*, *P. nodosus*, *P. illinoensis*, *H. dubia*, and *N. odorata*. Two treatments were examined for each plant species, including an insecticide treatment that eliminated most invertebrate herbivores and an untreated control that permitted natural development of invertebrate herbivore communities. The invertebrate herbivore impacts on the aquatic plants were quantified by comparisons of dry biomass of each species between treatments after one season's growth.

MATERIALS AND METHODS

Study Site and Design: The study was conducted at the Lewisville Aquatic Ecosystem Research Facility (LAERF) located in Lewisville, Texas (Denton County). The LAERF comprises 53 earthen ponds ranging from 0.2-0.81 ha in size and averaging 1 m in depth. Ponds were constructed in the 1950's with clay liners overlaid by sandy-loam topsoil, and were used as game fish production ponds until 1985. Native macrophytes and macroinvertebrates inhabit all ponds when flooded. Water is gravity-fed to the ponds from Lewisville Lake in Denton County, Texas (Smart 1995).

Two 0.3-ha ponds were used in this study. Preparation of the two ponds, hereafter designated treated and non-treated, included draining, mowing, rototilling, and refilling. Water levels were maintained with a constant low-flow and standpipe set at the drainage structure in each pond. In June 2004, after filling the ponds with approximately 30 cm of water, six replicates of five species of aquatic macrophytes were planted in each. Three species, *P. nodosus*, *P. illinoensis*, and *N. odorata*, characteristically support leaves that float on the water surface, while two species, *V. americana and H. dubia*, are almost entirely submersed. Each replicate was enclosed in a cylindrical cage, 91 cm in diameter by 122 cm tall, constructed from 2-in. × 4-in. (nominal size) mesh welded-wire fencing and anchored to the sediment with 30-cm lengths of rebar. Five plants grown in 4-in. (nominal size) commercial nursery pots were planted within each cage except *N. odorata*, in which three plants grown in nursery pots were planted. Twenty triploid grass carp were stocked in each pond to control endemic vegetative growth outside cages. Ponds were originally filled to a depth of approximately 61 cm to permit planting and rapid establishment of plants; after most had reached the surface, water levels were raised by 46 cm, and finally to a study depth of 122 cm.

The insecticide temephos (Abate, Clarke Mosquito Control Products, Inc., Roselle, IL), a non-systemic organophosphate, was used in the treated pond to eliminate a majority of invertebrate herbivores. Plants were treated with Abate weekly for three weeks at an application rate of 0.24 µL/L while in culture, prior to planting to ensure that insects were not introduced during planting. Thereafter, Abate was applied weekly at the same rate of 0.24 µL/L to the treated pond through a ½-in. (nominal size) diameter irrigation hose and drip emitter installed in each cage (Figure 1). The irrigation hose was attached to a gas-powered sprayer (FIMCO, No. Sioux City, SD), (Figure 2) for Abate application. Abate was not applied to the non-treated pond.

Data Collection and Sample Processing: Weekly observations of plant condition and herbivore damage were taken for each cage in each pond as an ongoing measure of plant growth and insect damage. In October 2004, the ponds were drained and all plant material within the cages removed, placed in mesh bags, and later washed with a low-pressure hose to dislodge any debris.

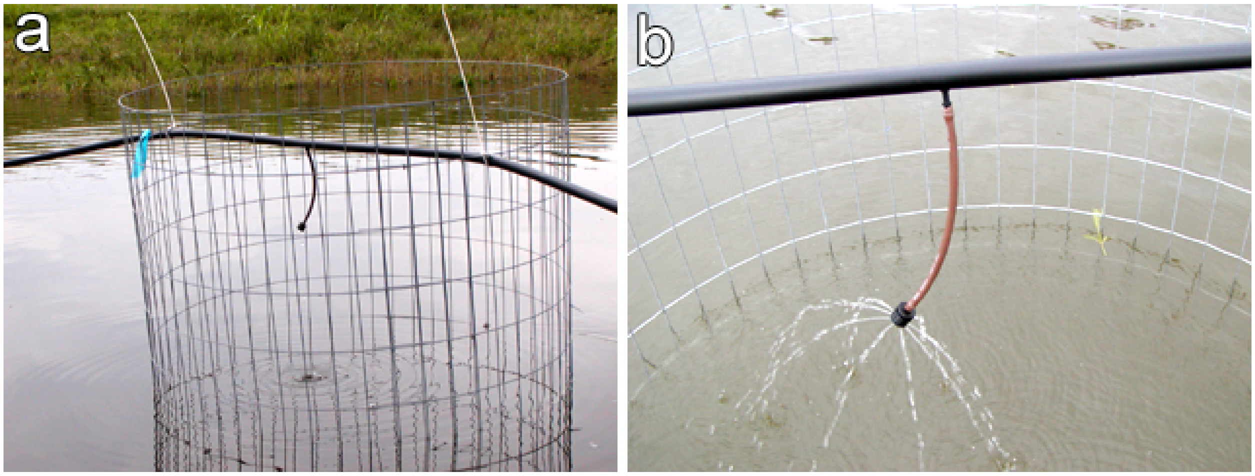

Figure 1. The Abate application system consisted of 1/2 –in.-diameter irrigation hose installed through each cage (a) with a drip emitter (b) in each cage.

Figure 2. Abate was applied to the treated pond by attaching irrigation hose to a gas-powered sprayer.

Plants from each cage were then separated into species and dried in a Blue-M forced air convection oven (General Signal, Atlanta, GA) at 55º C for a minimum of 48 hours before recording dry biomass.

STATISTICAL ANALYSIS: Experimental data were analyzed using Statistica (StatSoft 2002, Tulsa, OK) and include ANOVA, independent t-test, and correlation analyses. Unless otherwise noted, statements of significance made throughout the text refer to a 5 percent level or less of statistical confidence.

RESULTS AND DISCUSSION: Based on observations of plant condition, Abate successfully removed most herbivores from the treated pond. The treated plants had limited feeding and non-consumptive damage compared to the non-treated plants (Figures 3 and 4). Three insects were identified as causing the most damage to the non-treated plants; *Synclita obliteralis* larvae,

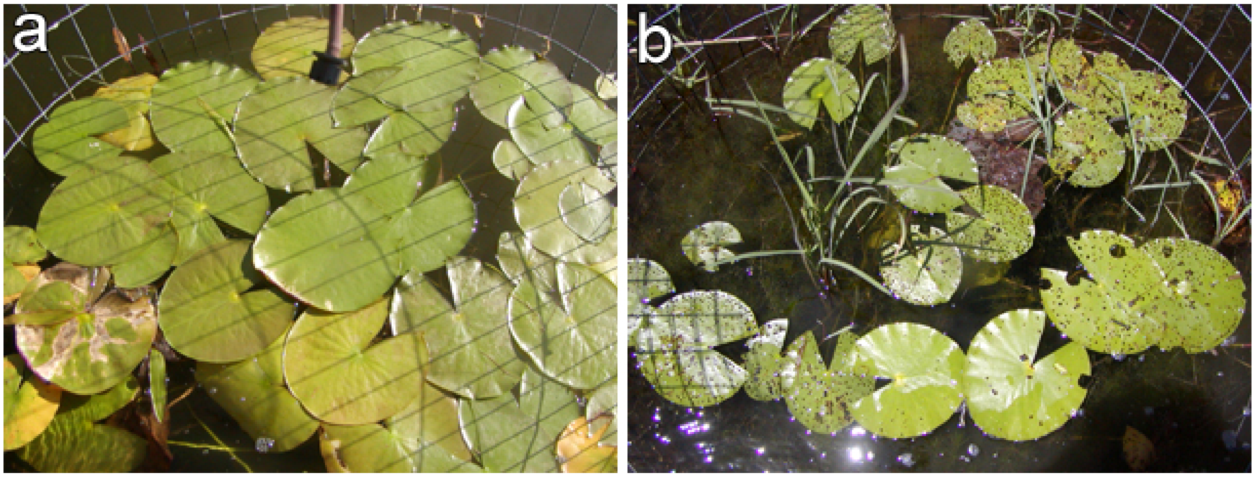

Figure 3. Treated (a) and non-treated (b) *N. odorata* at week 5 of the study. Final dry weights at week 17, N*. odorata* treated (a) = 129.7 g, non-treated (b) = 52.2 g, *C. vulgaris* treated (a) = 50.2 g, non-treated (b) = 0.0 g. No correlation existed between *N. odorata* and *C. vulgaris* dry weights. Damage from *Donacia* and *S. obliteralis* feeding can be seen in the non-treated floating leaves (b). The large semi-circular pieces removed from the floating leaves are used as cases for larval *S. obliteralis* (b).

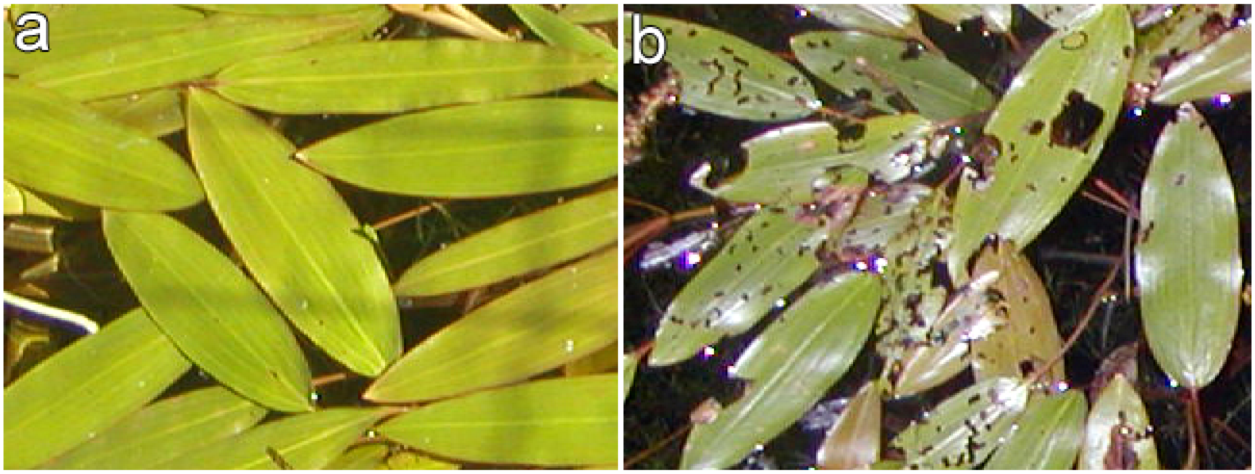

Figure 4. A close-up of treated (a) and non-treated (b) *P. nodosus* at week 5 of the study. Final dry weights at week 17, *P. nodosus* treated (a) = 139.5 g, non-treated (b) = 56.1 g, *C. vulgaris* treated (a) = 104.5 g, non-treated (b) = 6.5 g. No correlation existed between *P. nodosus* and *C. vulgaris* dry weights. Case making and feeding damage by *S. obliteralis* can be seen in the non-treated leaves (b).

a *Donacia* spp., and the oviposition by various species of odonates. *Synclita obliteralis* fed on *P. nodosus, P. illinoensis,* and *N. odorata* in the non-treated pond (Figure 5). This lepidopteran is a generalist feeder known to feed on at least 60 different aquatic plants (Center et al. 1999). Larvae reside in free-floating portable cases and construct cocoons within the cases for pupation. Pupal cases are attached to petioles or leaf blades for the duration of pupation. *Synclita obliteralis* was found in large quantities throughout the study in or near the cages of the three floating leaved species.

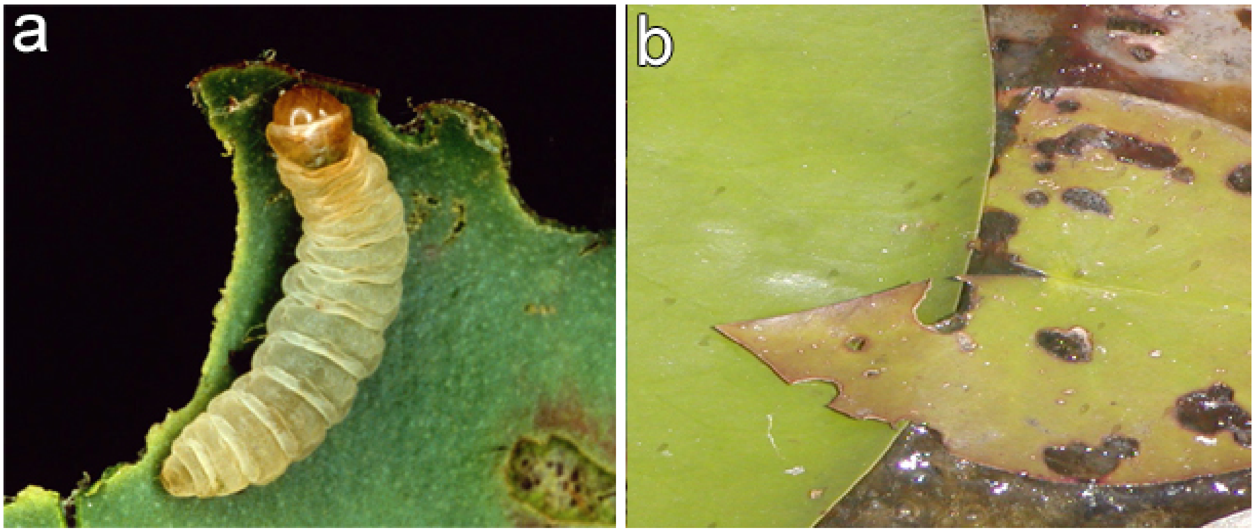

Figure 5. *S. obliteralis* larva removed from its case (a), (Center et al. 1999). *S. obliteralis* case making and feeding damage to a *N. odorata* leaf (b).

Donacia adults and eggs were readily found on *N. odorata*, but not observed on any other macrophyte species (Figure 6a). Unfortunately, the life histories of the longhorned leaf beetles contained in the genus *Donacia* are not well described, yet most are known to be generalist feeders (Center et al. 1999). However, despite not identifying the *Donacia* encountered to species, it apparently exhibits selective feeding, at least among the plants available in the study ponds. Adults fed on emergent leaves of *N. odorata* and remain on vegetation above the water's surface while larvae either migrate to the sediment to feed on roots and rhizomes or feed on submersed leaves and stems. Females have diverse methods of ovipositing (Center et al. 1999), but only one method was observed during this study. Eggs were oviposited in concentric rows on the underside of emergent leaves, through a hole chewed in the leaf (Figure 6b). Larvae and pupae were not observed during the four months of this study. This could be due to the fact that some *Donacia* larvae require a year or more before pupation (Center et al. 1999).

Most Zygopterans and two Anisopteran families, Aeshnidae and Petaluridae, are known to deposit eggs in plant stems and leaves (Figure 7). This endophytic trait can result in excessive damage to plant tissue when large numbers of females are present (Westfall and Tennessen 1996). Eggs were found in *P. nodosus, P. illinoensis, and N. odorata*. Eggs were deposited in shallow indentions in the plants' leaves, leaving holes after larvae emerged. These holes were numerous and sometimes completely covered a leaf's surface.

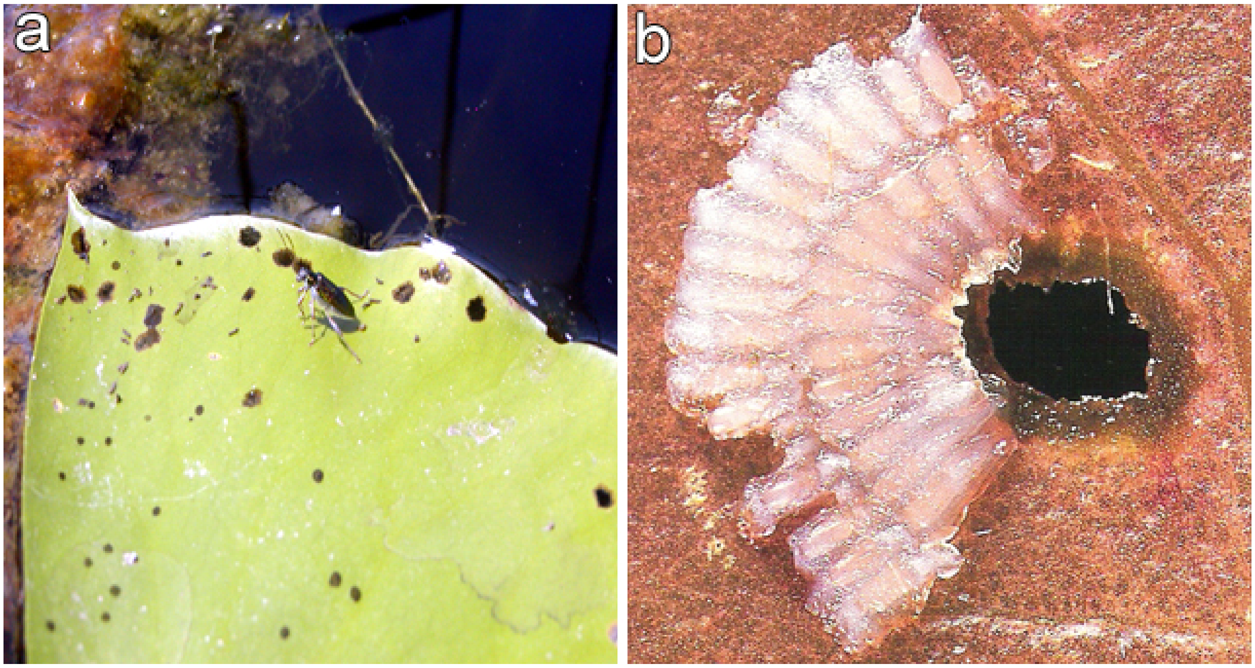

Figure 6. *Donacia* adult resting on a *N. odorata* leaf (a). *Donacia* eggs oviposited in concentric circles on the underside of a *N. odorata* leaf (b) (Center et al. 1999).

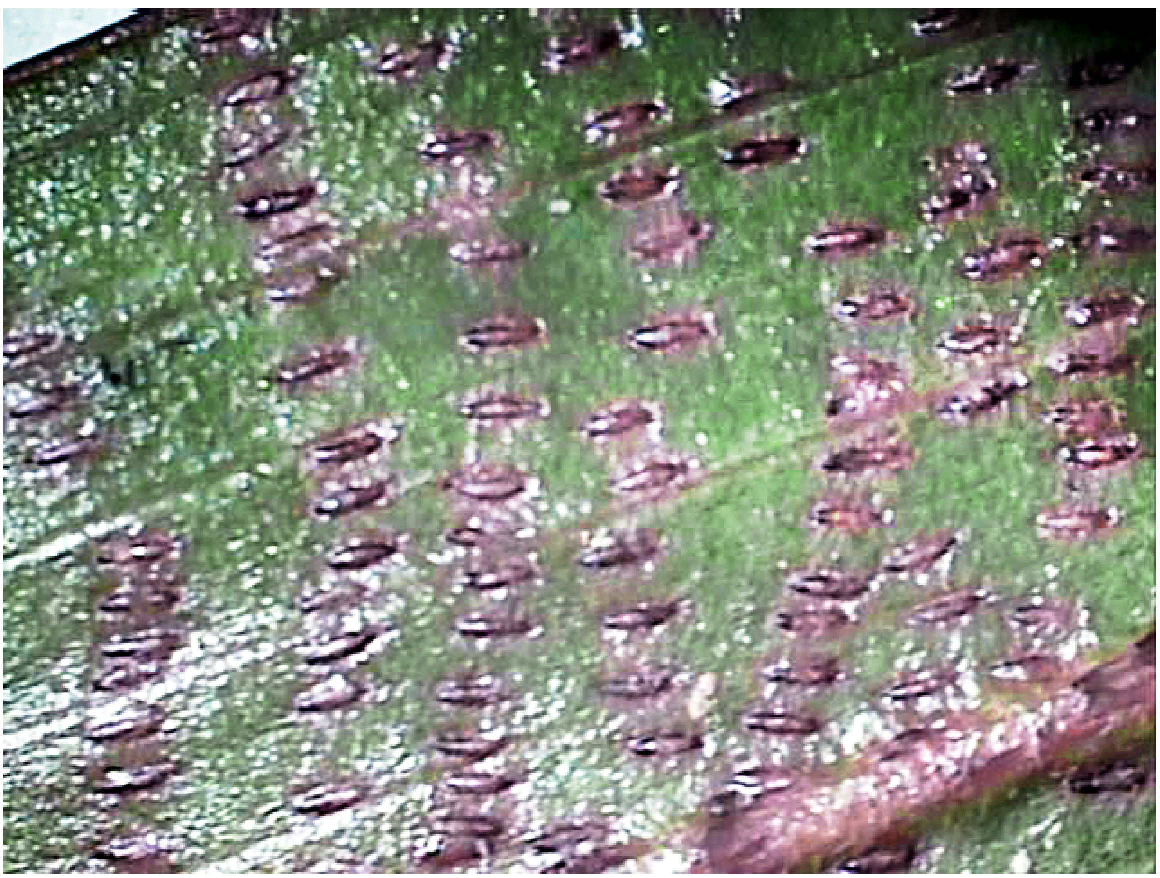

Figure 7. Odonate eggs on the underside of a *P. nodosus* leaf. After emergence, the leaf will be left with numerous holes.

Removal of herbivores using Abate resulted in a significant increase in macrophyte biomass for floating leaved species (Figure 8). This increase was over twofold higher for plants treated with Abate compared with those that received no insecticide. Although all three floating leaved species displayed this trend, only *P. nodosus* exhibited significance at p = 0.05 (Figure 9). Extensive damage by herbivores was observed on *P. nodosus* in the non-treated pond throughout the study (Figure 4b) and mean dry weights were 2.5 times higher in the Abate treated pond (Figure 9). Apparently, the dry biomass differences to *P. nodosus* were due to insect herbivory and non-consumptive damage such as odonate eggs.

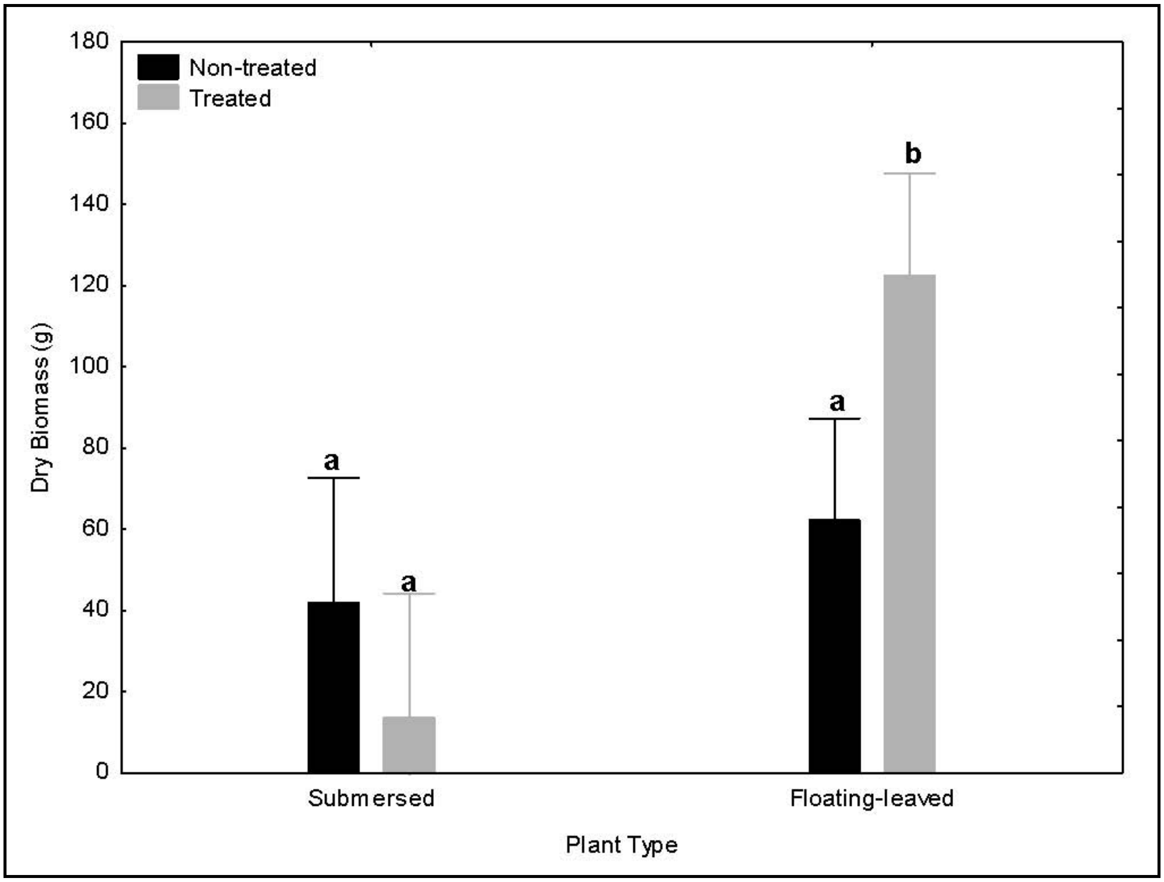

Figure 8. Mean (± 0.95 confidence interval) dry weights of submersed and floating-leaved species in treated and non-treated ponds. Means with the same letter are not significantly different at p = 0.05 for means within the same plant type. A planned comparison using contrasts separated the treatments within plant types, (2-way ANOVA, treatment: p = 0.261, df = 1, 56; F = 1.291, plant type: p = 0.000, df = 1, 56; F = 21.288, interaction: p = 0.002, df = 1, 56; F = 10.044).

Significant differences in mean dry weights were not found for the two other floating leaved species, although *N. odorata* and *P. illinoensis* exhibited from 1.6 to 2.8-fold greater biomass, respectively, in the pond where herbivores were eliminated (Figure 9). Substantial amounts of herbivory and non-consumptive damage were observed throughout the study on both of these species in the non-treated pond (Figures 3b and 10b). *Donacia* were commonly found on floating leaves of *N. odorata*,

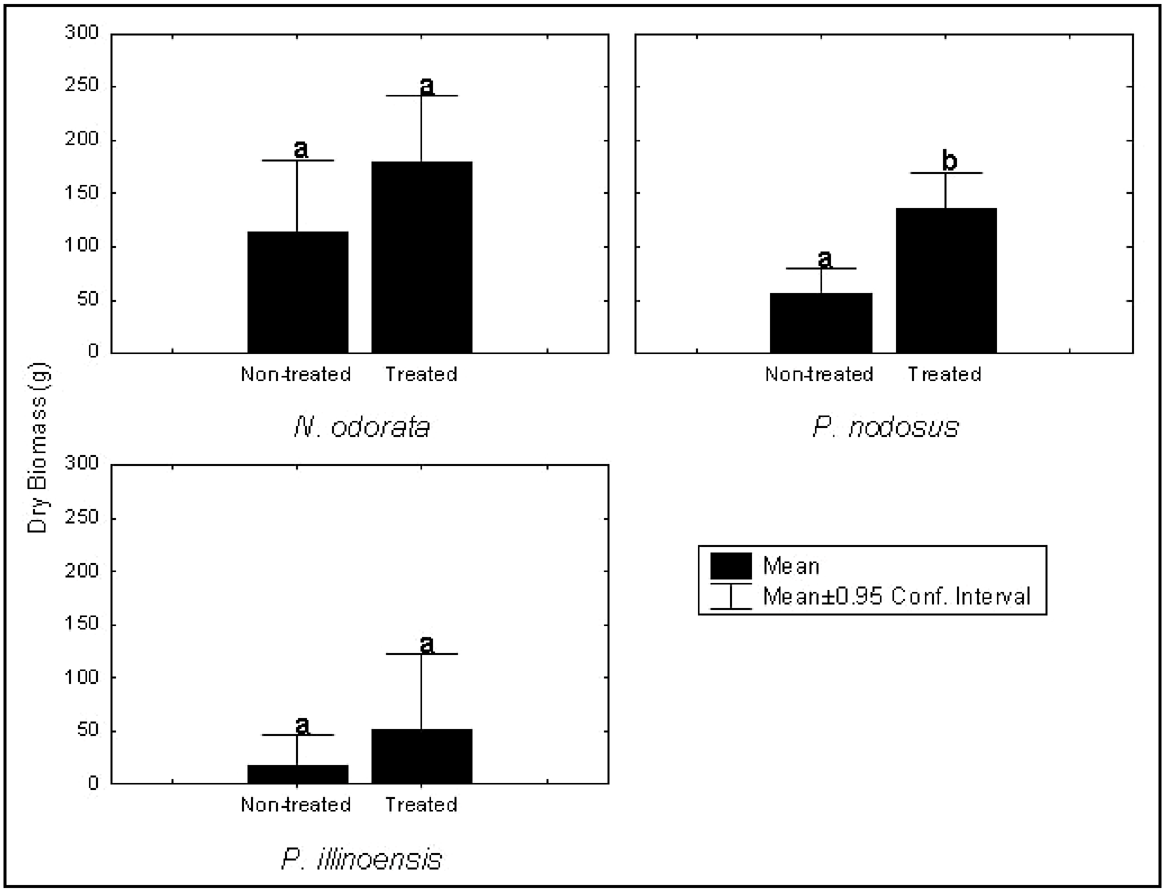

Figure 9. Mean dry weights (± 0.95 confidence interval) of floating-leaved species in treated and non-treated pond. Means with the same letter are not significantly different at $p = 0.05$ level for means within the same species. Mean dry biomass of *N. odorata* and *P. illinoensis* were not significantly different in the treated pond (independent t-test, $p = 0.090$ and $p = 0.290$, respectively) while mean dry biomass of *P. nodosus* was significantly greater in the treated pond (independent t-test, $p = 0.001$).

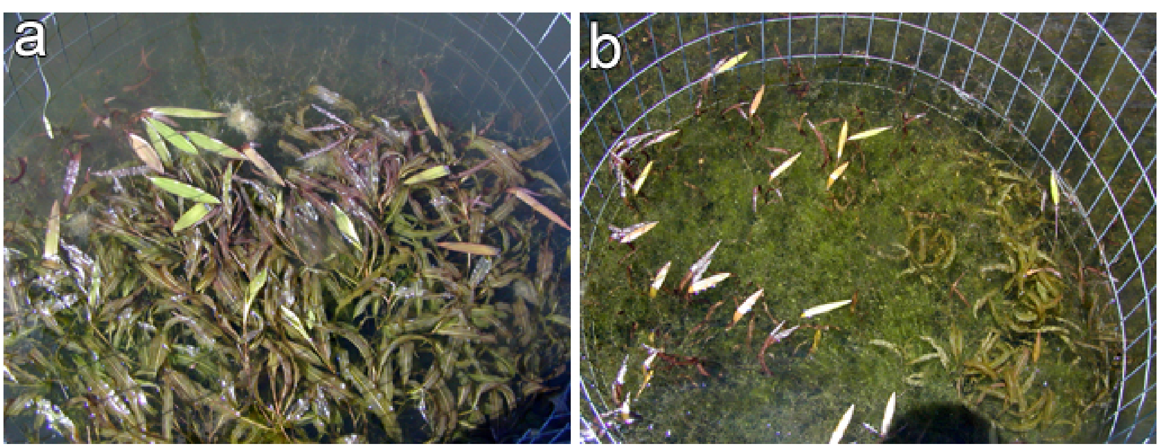

Figure 10. Treated (a) and non-treated (b) *P. illinoensis* at week 5 of the study. Final dry weights at week 17, *P. illinoensis* treated (a) = 15.9 g, non-treated (b) = 8.9 g, *C. vulgaris* treated (a) = 99.8 g, non-treated (b) = 10.9 g. No correlation existed between *P. illinoensis* and *C. vulgaris* dry weights.

while *S. obliteralis* was found on floating leaves of both species. Although floating leaves of *P. illinoensis* were highly damaged by herbivores in the non-treated pond, evidence of damage to submersed leaves was rare.

In contrast, no significant biomass differences were detected for the submersed species (Figure 8). Consumptive as well as non-consumptive invertebrate damage was rare on *V. americana* and *H. dubia* in both the treated and non-treated ponds, yet herbivore damage has been observed on both species while in culture at the LAERF.[1] It is possible that herbivores feeding on these two submersed species were unable to colonize the ponds within the experimental time frame of four months. Interestingly, contrary to what was observed for the floating-leaved species, submersed plant biomass means were reduced 45 and 90 percent (*H. dubia* and *V. americana*, respectively) in Abate-treated ponds (Figure 11). A possible explanation was competition and shading from *Chara vulgaris* L., which grew profusely in the Abate-treated pond, but less so in the non-treated pond: mean dry weights of *C. vulgaris* found in the study were 11 times greater in the treated pond (Figure 12).

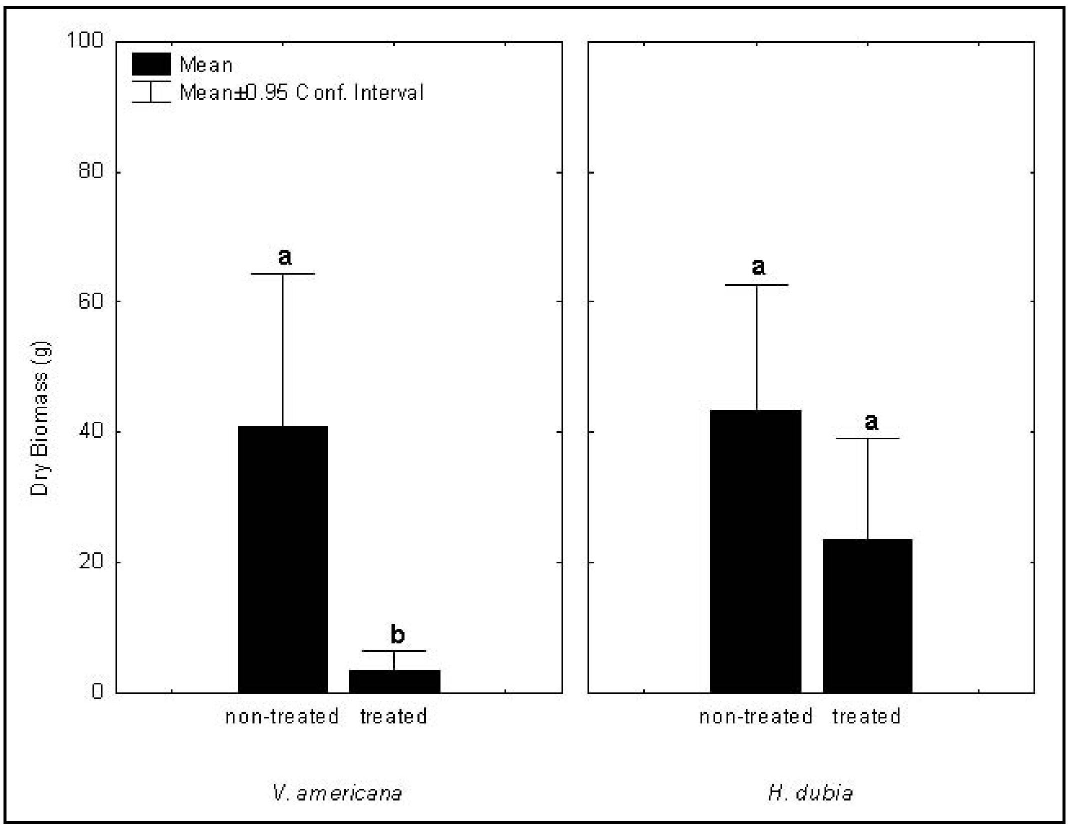

Figure 11. Mean (± 0.95 confidence interval) dry weights of submersed species in treated and non-treated ponds. Means with the same letter are not significantly different at p = 0.05 level for means within the same species. Mean dry biomass of *V. americana* was significantly less in the treated pond (independent t-test, p = 0.002), while no significant differences in mean dry biomass of *H. dubia* were detected (independent t-test, p = 0.068).

[1] Personal communication. 2006. Dr. Gary O. Dick, U.S. Army Engineer Research and Development Center, Lewisville, TX.

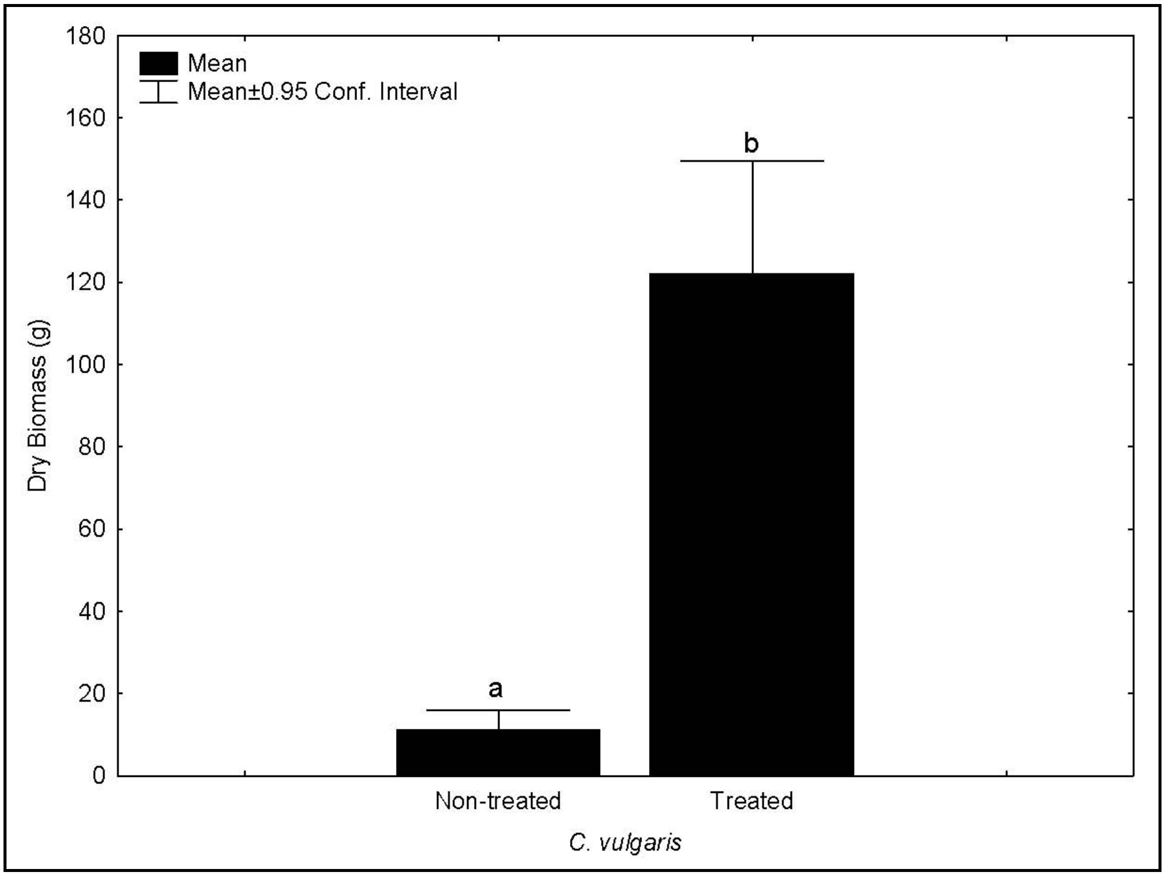

Figure 12. Mean dry weights (± 0.95 confidence interval) of *C. vulgaris* in treated and non-treated pond. Means with the same letter are not significantly different at p = 0.05. Mean dry biomass of *C. vulgaris* was significantly greater in the treated pond (independent t-test, p = 0.000).

Because this macroalga occupied the entire water column, it may have had a competitive advantage for light over *V. americana*, which grew closer to the substrate. In the treated pond, a typical cage of *V. americana* was dominated by *C. vulgaris* throughout the water column and the entire surface (Figure 13a). On the other hand, *H. dubia* occasionally reached the surface but the cages were still dominated by *C. vulgaris* (Figure 13b). Spatial or nutrient competition may have played a role in reduced growth of *H. dubia*. Reasons for such large differences are unknown but may be related to an increase in over-wintering *C. vulgaris* spores in the treated pond, nutrient or other environmental differences between ponds, selective herbivore pressures, or the difference may have been treatment related, due to elimination of unknown herbivores of *C. vulgaris*. A Pearson correlation analysis revealed a strong negative correlation between *V. americana* and *C. vulgaris* dry biomass (Figure 14). However, a similar correlation was not observed for *H. dubia* or any of the floating leaved species.

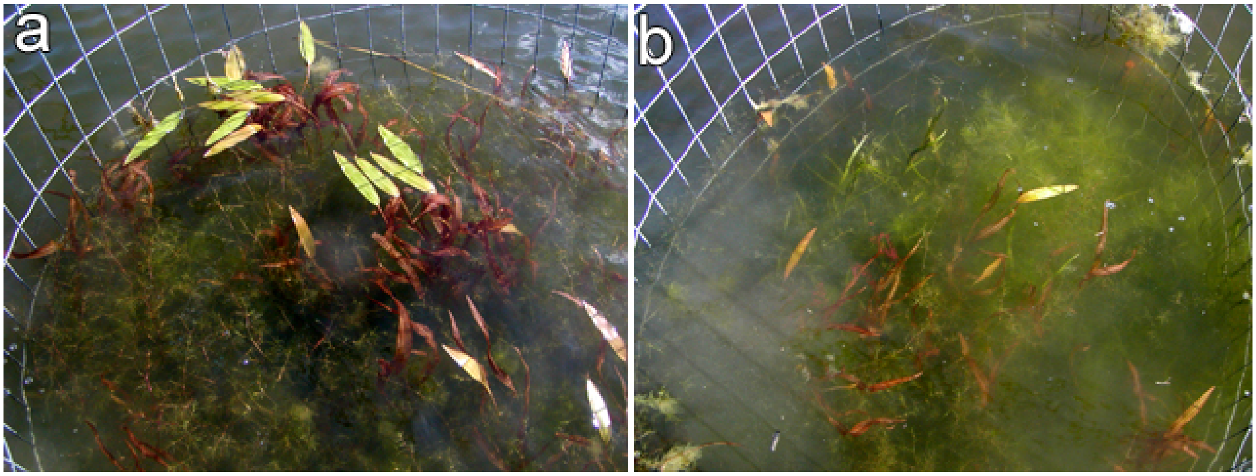

Figure 13. Treated cages of *V. americana* (a) and H. dubia (b) at week 5 of the study. Final dry weights at week 17, *V. americana* treated (a) = 0.9 g, *H. dubia* treated (b) = 8.2 g, *C. vulgaris* (a) = 115.3 g, and (b) = 84.4 g. No correlation existed between *H. dubia* and *C. vulgaris* dry weights.

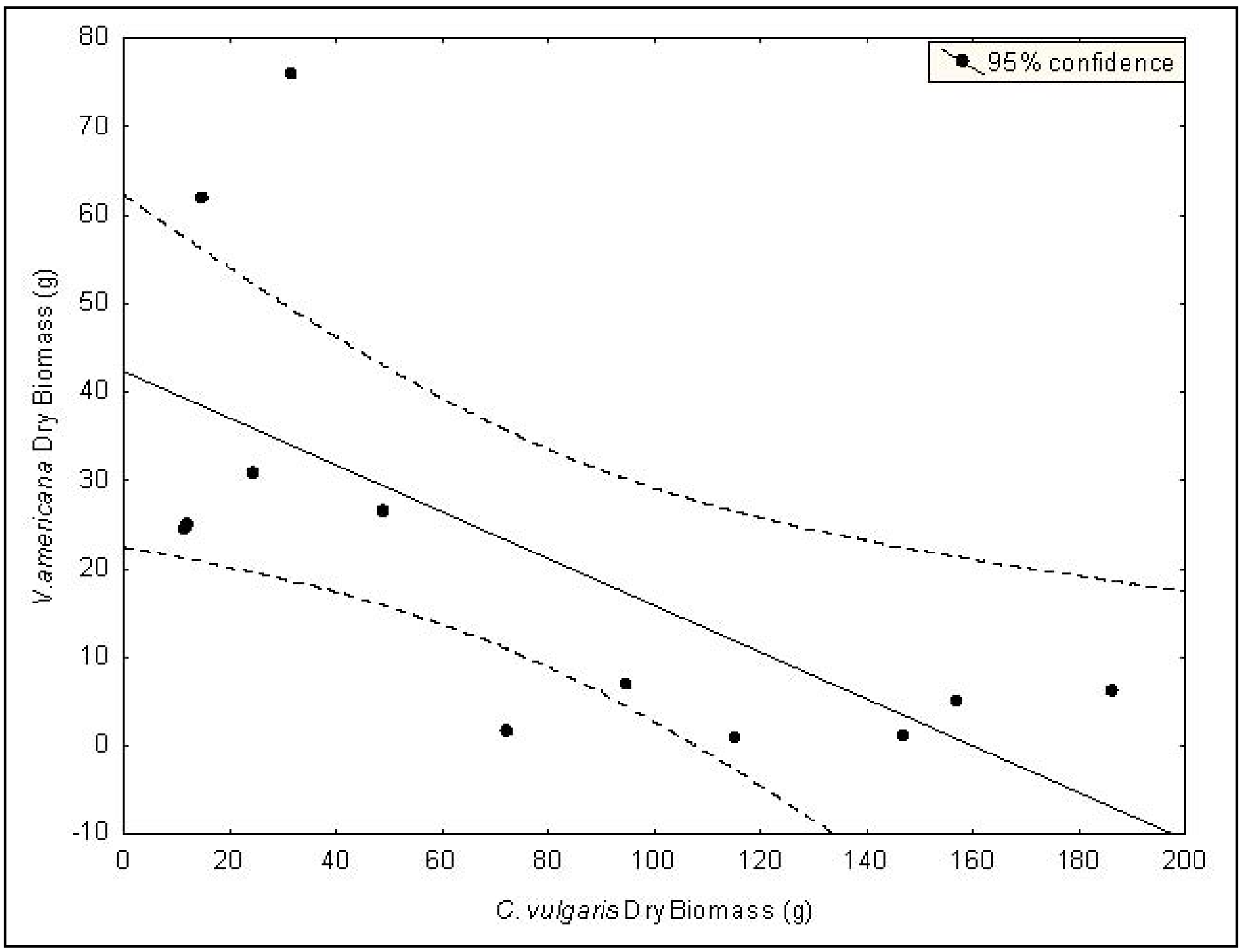

Figure 14. Pearson correlation analysis between the dry weights of *V. americana* and *C. vulgaris* ($p < 0.050$, $r = -0.67$).

Differences in algal growth were observed throughout the study and may have been due to nutrient differences between treatments. Filamentous algae were altogether absent in the treated pond (Figure 15a). Removal of herbivores in the treated pond resulted in increased plant growth of some species. The actively growing plants may have utilized most available nutrients and in return hindered the ability of algae to attain nutrients required for growth. In contrast, filamentous algae grew profusely in the non-treated pond. At times the algae covered the entire pond's surface, but were displaced and condensed into the margins due to wind action (Figure 15b). Most plants in the non-treated pond were highly damaged due to invertebrate herbivory as well as non-consumptive damage. This reduced the plant's ability to grow and increased the amount of decaying plant matter that may have released nutrients, facilitating algal growth.

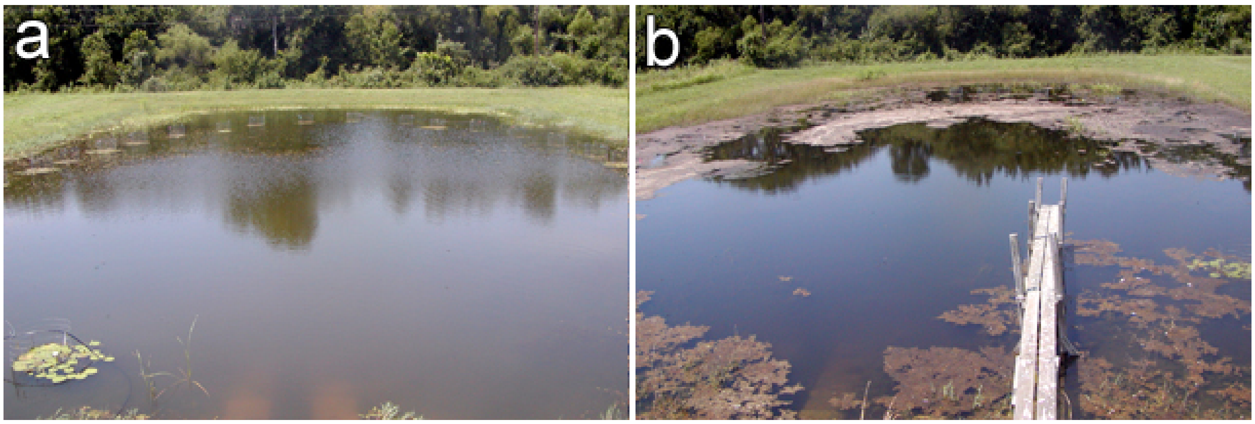

Figure 15. Treated (a) and non-treated (b) ponds at week 9 of the study. Filamentous algae were absent in the treated pond (a), but grew profusely in the non-treated pond (b). The algae grew throughout the entire water's surface in the non-treated pond (b), but were displaced and condensed into the margins due to wind action.

FUTURE STUDIES: The large amounts of *C. vulgaris* biomass in the insecticide-treated areas of the current study were not fully understood. One possible explanation is that an herbivore of *C. vulgaris* was eliminated by the insecticide application. A survey of invertebrates associated with *C. vulgaris* could answer questions on the magnitude of herbivory in association with this species. Criteria for possible survey areas could include ponds or lakes where *C. vulgaris* has grown naturally for many years.

Further research conducted in the summer of 2005 examined interactions between invertebrate herbivores and four species of aquatic plants: *V. americana*, *P. nodosus*, *P. illinoensis*, and *N. mexicana* using methodology to eliminate the possibility that differences detected in this study were artifacts of environmental differences between ponds. The species were planted in three ponds, each divided by a fence covered in pond liner, allowing Abate application to only one side of each pond. The insecticide applications to one-half of each pond allowed differentiation of pond and treatment differences. Herbivory was then quantified by comparisons of dry biomass per species between insecticide and control specimens. Invertebrate populations were also quantified to assess the ability of Abate to remove invertebrates and to identify herbivores for possible use as biocontrol agents. Analysis of these data is not yet complete.

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